BULLETIN OF MARINE SCIENCE, 28(4): 716–727, 1978

FISHES OF THE FAMILY OPHIDIIDAE. IX. ANALYSIS OF GEOGRAPHIC VARIATION IN *LEPOPHIDIUM MICROLEPIS* WITH DESCRIPTIONS OF TWO NEW SUBSPECIES

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ABSTRACT

Lepophidium microlepis ranges from Baja California to Peru, a distribution shared with *L. negropinna* and *L. pardale.* Unlike its more shallow-dwelling congeners, *L. microlepis* exhibits marked latitudinal variation in meristic and morphometric characters and in certain features of pigmentation. Three well marked subspecies are defined, two of which, *L. microlepis hubbsi* and *L. microlepis inca,* are described as new.

The isolating mechanisms involve the fact that adults of *microlepis* occur in cold waters of the deep shelf and upper slope while the larvae require warm surface waters as do all species of *Lepophidium.* Unfavorable surface currents which move larvae offshore, surface temperature and its annual variation, poleward-flowing undercurrents, and physiographic features of the Continental Shelf itself are all discussed as factors in maintaining stock isolation of one or all of the subspecies.

Surface currents are judged to be most important in isolating *microlepis* from *hubbsi.* Reasons for the isolation of *hubbsi* and *inca* are less clear but probably involve the marked difference in surface temperatures between the range of the two as well as surface currents and possibly the Peru-Chile Undercurrent.

The authors have studied all available material of *Lepophidium microlepis,* including much that was unavailable to Robins (1962), and find it divisible into three subspecies, two of which are described as new. A discussion of both the geographic and bathymetric distributions of these forms is included. Few variational studies of fishes of this region have been published and none, to our knowledge, involves a species of the deeper half of the Continental Shelf.

Abbreviations used in the tables and text are: CAS = California Academy of Sciences, San Francisco; GCRL = Gulf Coast Research Laboratory, Ocean Springs, Mississippi; IMARPE = Instituto del Mar del Peru, Callao, Peru; LACM = Los Angeles County Museum of Natural History, Los Angeles, California; SIO = Scripps Institution of Oceanography, La Jolla, California; SOSC = Smithsonian Oceanographic Sorting Center, Washington, D.C.; SU = Stanford University Natural History Collections (now housed at the California Academy of Sciences); UCLA = University of California, Los Angeles; UCR = Universidad de Costa Rica, San Jose, Costa Rica; UMML = Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida; UP = Universidad de Panama, Panama City, Panama; USNM = National Museum of Natural History, Washington, D.C. Measurements are as defined by Robins (1962: 487–488). In the listing of material, the number of specimens and their range in standard length are placed parenthetically following the museum numbers.

Lepophidium microlepis (Gilbert)
Tables 1–2, Figure 1

Synonymy.—See Robins (1962: 494), all references of which apply to the nominate subspecies. The first citation in the 1962 synonymy should be "*Leptophidium microlepis* Gilbert, 1890: 109" instead of "*Lepophidium microlepis* . . ." Subsequent references are given below under the account of each subspecies.

Diagnosis.—Head and body rather uniformly dusky, paler (sometimes silvery white) along the belly. Vertical fins unmarked except for a dark edge which is variously developed in

the different subspecies. Peritoneum silvery; esophagus black, stomach pale, pyloric caeca and hind gut pale to blackish. Gill chamber, the floor of the mouth and anterior part of the mouth, pale. Pharyngeal region as far back as the pseudobranchs pale to black. Numbers of fin rays, gill rakers, vertebrae and pyloric caeca, and measures of body parts are given in Tables 1 and 2.

Comparisons.—*Lepophidium microlepis* is easily distinguished from other Pacific species of *Lepophidium* except *L. stigmatistium* by pigmentary differences (Robins, 1962: fig. 1, and the key, p. 488). *L. stigmatistium* has a small but distinctive blackish area in the dorsal fin between rays 4 and 14 and has fewer pectoral rays (19–21) and more gill rakers (18–20). It also has the gill chamber entirely black except for the gill bars.

Lepophidium microlepis microlepis (Gilbert)
Tables 1–2, Figure 1

Synonymy.—See Robins (1962).

Diagnosis.—Caudal vertebrae 51–55, usually 52–53, total vertebrae 66–70, usually 67–69; dorsal-fin rays 117–128, anal-fin rays 97–108. Pyloric caeca 5–6 (rarely 7 or 8). Juveniles with narrow dark edge to vertical fins; in adults, this feature largely absent from the dorsal fin and narrow and inconspicuous in the anal fin. Pectoral fins unpigmented. Entire orobranchial cavity usually pale but some specimens with rear of roof of mouth dusky. Esophagus black but stomach and hind gut pale.

Material examined.—SIO 60-465-61 (1, 156) Lat. 26°12.5–13.8′N, Long. 113°18.2–22.7′W in 91 m, 2 Dec. 1960. SIO 60-466-61A, Lat. 26°04.5–05.9′N, Long. 113°34.0–35.5′W in 228–293 m, 2 Dec. 1960. SIO 61-171-61A (12, 134–163), Lat. 25°43–34.5′N, Long. 112°51.4–53′W in 115–221 m, 2 May 1961. SIO 65-227-61A (16, 104–220) Lat. 24°12.3–09.5′N, Long. 111°29.7–25.0′W and Lat. 24°11.4–10.0′N, Long. 111°28.5–25.3′W in 102–106 m, 27 June 1965. SIO 65-268-61A (1, 160) Lat. 24°59.8–58.2′N, Long. 110°42.7–42.0′W in 210 m, 8 July 1965. SIO 65-275-61B (4, 229–246) Lat. 24°58.2′N, Long. 110°42.0′W in 210 m, 8 July 1965. SIO 68-103-61 (7, 109–164) Lat. 28°19.3–20.1′N, Long. 112°08–10.5′W in 293–307 m, 21 Jan. 1968. SIO 73-2 (1, 186) Lat. 28°27′N, Long. 112°22′W in 270 m, 12 Nov. 1972. LACM 31769-6 (1, 154), Lat. 24°14′N, Long. 111°32′W in 106 m, R/V SEARCHER sta. 28, 1 Feb. 1971. LACM 32043-10 (1, 193) Lat. 28°19′25″N, Long. 115°09′45″W in 73 m, R/V SEARCHER sta. 243, 19 Oct. 1971.

Types.—The syntypic series was a complex of two species, only three specimens of which are *L. microlepis* as restricted by Robins (1962). Robins (1962: 495) designated USNM 44390 (1, 248) as lectotype and reidentified SU 219 (5, 133–220), the remainder of what was thought to be the total syntypic series, with *L. negropinna.* In the addendum (p. 495), Robins discussed USNM 73409 (2, 162–234) but made no comment on its type status. Despite its higher catalog number, it was collected at the same ALBATROSS station (3015) as the lectotype, and there is no reason not to consider these two specimens as syntypes. They are here designated paralectotypes of *L. microlepis.* Similarly, USNM 197144 (5, 179–333), specimens correctly reidentified by Robins as *L. negropinna,* were supposedly collected at the same station (3015) and no doubt were also part of the original syntypic series of *microlepis.* It is likely that they came from the shallower station 3016 as did other material of *negropinna.* Both USNM 197144 and SU 219 are paralectotypes of *microlepis* even though they are correctly assigned to *L. negropinna.*

Distribution.—*L. m. microlepis* is known both from the Gulf of California and from the outer coast of Baja California as far north as Bahía Sebastián Viscaíno. Within the Gulf the species ranges in depth from 210 to 307 m whereas along the outer coast it occurs between 73 and 293 m. Both sets of depth data are consistent with bottom temperatures of 10–12°C (Hubbs and Roden, 1964).

The northward limit of distribution apparently is controlled by cold surface waters which prevent completion of the early life history which is completed in surface or near-surface waters. This is the opposite of the condition required by scorpionfishes of the cold temperate genus *Sebastes,* in which

Table 1. Measurements of body parts expressed in percent of standard length for selected specimens of *Lepophidium m. microlepis*, *L. m. hubbsi* and *L. m. inca* (for definition of measurements see Robins, 1960: 90–91)

	microlepis											
Measurement	LACM 31769	SIO 60–465	SIO 60–466	SIO 65–268	SIO 60–466	SIO 73–2	LACM 32043	SIO 65–275	SIO 65–275	SIO 65–275	SIO 65–275	USNM 44390
Standard length mm	153.5	156.3	158.9	160.4	183.2	186.5	193.2	229.0	230.1	237.3	246.5	248.0*
Head length†	25	25	26	23	23	23	22	24	26	26	25	23
Snout tip to:												
dorsal fin	28	26	28	26	25	26	24	28	28	29	28	27
anal fin	43	43	41	38	36	41	39	43	41	41	46	40
occiput	17	16	17	15	15	16	15	14	14	16	15	15
end of lateral line	88	82	88	88	90	91	88	91	90	91	90	85
tip maxilla	11	10	11	10	9.9	11	10	10	11	12	12	10
Body depth at:												
occiput	14	16	14	12	13	13	10	14	14	14	14	12
dorsal fin origin	15	16	15	16	15	15	11	16	16	17	16	15
anal fin origin	13	12	11	13	11	12	13	13	14	13	13	12
Pectoral fin	12	10	11	10	11	10	9.6	12	11	11	11	10
Pelvic Ray:												
outer	6.6	–	6.8	6.4	6.2	7.2	5.1	7.2	7.6	8.0	7.7	6.6
inner	4.8	–	4.7	4.6	3.9	4.3	3.3	4.8	5.5	5.8	–	4.8
Orbit Diameter	6.1	5.6	5.8	5.9	5.1	6.2	5.0	5.8	5.4	6.0	5.5	6.0
Bony interorbit	3.1	3.1	3.3	3.1	2.7	2.8	2.9	3.1	3.1	3.3	3.1	3.0
Snout length	4.7	4.3	4.4	4.0	4.0	4.0	4.3	3.9	4.6	4.6	4.7	3.9
Postorbit	15	15	16	14	14	13	12	15	16	16	15	13
Sex	?	♀	♀	♀	♀	♀	?	♂	♀	♂	♀	♂

Table 1. (Continued)

	hubbsi													
Measurement	UCR-328	UP 807	GCRL 13965	UCR-328	UP 807	UCR-328	GCRL 13965	GCRL 13965	LACM 85772-1	GCRL 13965	GCRL 13965	UMML 32882	GCRL 13965	UMML 32229
Standard length mm	166.5	169.0	169.5	178.5	189.0	195.1	198	200.0	209.0*	209.6	211.0	211.5	217.0	232
Head length†	24	23	23	25	22	24	23	23	23	24	23	23	22	24
Snout tip to:														
dorsal fin	25	24	24	24	24	24	25	24	24	25	23	24	24	27
anal fin	40	39	41	41	38	39	39	40	37	39	39	40	40	40
occiput	15	16	15	15	15	16	16	16	16	15	15	15	15	18
end of lateral line	92	89	96	92	93	92	92	91	92	90	95	93	92	93
tip maxilla	10	10	11	11	10	11	10	10	10	12	10	11	10	11
Body depth at:														
occiput	13	12	12	13	13	13	12	14	14	14	14	14	14	14
dorsal fin origin	14	12	15	–	–	14	13	15	15	14	14	14	14	15
anal fin origin	12	11	16	11	13	12	10	12	12	11	11	12	12	12
Pectoral fin	13	12	11	13	12	12	12	12	12	12	12	11	11	13
Pelvic Ray:														
outer	6.8	6.5	6.8	6.8	7.8	7.5	7.4	8.4	7.2	6.9	7.3	6.1	6.7	8.1
inner	4.6	4.6	3.7	4.5	5.1	4.9	5.1	6.0	4.6	4.2	4.9	4.7	4.3	5.4
Orbit Diameter	6.1	5.7	6.4	5.8	6.1	5.4	5.4	5.6	5.7	6.8	5.4	5.7	5.7	5.3
Bony interorbit	3.4	3.7	3.5	3.6	3.4	3.6	3.3	3.6	3.4	3.3	3.2	3.2	3.2	3.7
Snout length	4.0	4.0	4.3	4.5	3.4	4.2	4.6	4.5	3.8	3.9	4.2	4.4	4.7	4.4
Postorbit	14	13	13	14	12	13	13	13	14	13	13	13	12	10
Sex	♀	?	♂	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	?

Table 1. (Continued)

	inca										
Measurement	USNM 216346	UMML 32871	UMML 32871	USNM 216346	IMARPE	UMML 32871	UMML 32871	UMML 32871	USNM 216346	USNM 216346	USNM 216345
Standard length mm	163.0	165.2	170.7	171.0	171.0	171.6	177.2	177.6	186.0	191.0	193.8*
Head length†	22	21	21	21	21	22	21	22	21	21	21
Snout tip to:											
dorsal fin	24	23	23	22	24	24	24	24	23	24	23
anal fin	37	37	37	37	35	38	38	38	38	38	37
occiput	15	14	14	14	14	14	14	14	14	14	14
end of lateral line	89	92	94	89	87	91	92	90	88	91	91
tip maxilla	10	10	10	9.2	10	10	10	10	9.2	10	10
Body depth at:											
occiput	13	12	12	11	12	12	12	13	12	12	12
dorsal fin origin	14	12	12	11	12	12	14	14	12	13	13
anal fin origin	10	11	11	10	12	11	12	11	11	12	12
Pectoral fin	12	10	10	11	12	11	11	9.4	11	10	11
Pelvic Ray:											
outer	6.6	5.0	6.0	6.0	5.8	6.0	6.0	5.9	6.0	6.4	5.8
inner	4.0	3.3	3.7	4.1	3.8	4.4	3.8	3.9	4.0	4.1	3.6
Orbit Diameter	5.5	5.9	5.8	5.0	6.1	5.8	6.0	6.0	4.6	4.7	55
Bony interorbit	3.1	3.1	3.3	3.2	3.1	3.2	3.2	3.4	3.3	3.1	3.3
Snout length	3.9	3.8	3.8	3.7	3.2	3.9	4.0	3.9	4.0	4.4	3.7
Postorbit	12	12	12	12	13	12	10	13	12	12	12
Sex	♂	♂	♂	?	♂?	♀	♂	♀	♂	♂	♂

† To tip of opercular flap
* Lectotype (*microlepis*) or holotype (*hubbsi* and *inca*)

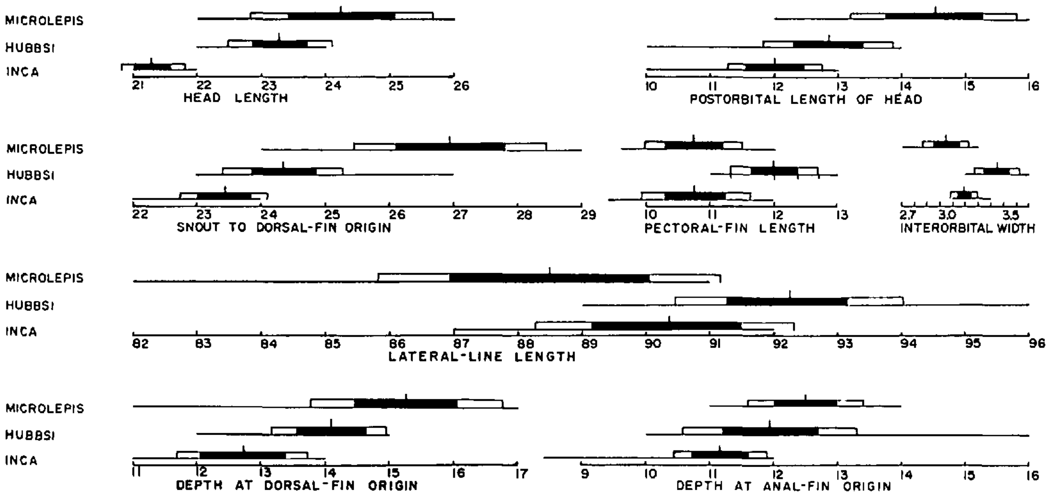

Figure 1. Sample comparison diagrams of selected measurements of adults of *Lepophidium microlepis*, *L. m. hubbsi* and *L. m. inca*. Numbers are of percent of standard length. Sample sizes are 12, 14, and 11 respectively.

the Gulf of California endemic species can find suitably cold surface waters only in the vicinity of Ballenas Channel (Chen, 1975: 136). The southern shore of Bahía Sebastián Viscaíno was noted by Hubbs (1960: 145) to be the northern limit of many tropical species, and *Lepophidium microlepis* would fall into this category if one considers the eggs and larvae which occur in surface waters. Otherwise the cold temperatures (10°–12°C) preferred by the deep-dwelling adults would allow this species to invade coastal waters of California to a major extent.

L. m. microlepis, when adult, evidently is a stenothermic, eurybathic form selecting temperatures between 13° and 10°C and thus occurs below the thermocline. Early stages of development require warm surface waters and these two factors combine to restrict its distribution.

We find minor differences in meristic characters between samples from the two sides of the Gulf of California suggesting that there is little if any genetic exchange between *L. microlepis* in the two regions. We do not accord the two populations taxonomic recognition.

Lepophidium microlepis hubbsi new subspecies
Tables 1–2, Figure 1

Diagnosis.—Caudal vertebrae 57–59, total vertebrae 71–73, dorsal-fin rays 128–134, anal-fin rays 108–112. Pyloric caeca 5–8. Juveniles and adults with conspicuous though somewhat diffuse dark border to the vertical fins. Pectoral fins dusky, especially basally. Roof of mouth from just inside palatine and vomerine teeth to pseudobranch and the upper pharyngeal region blackish, the area sharply defined. Gill bars also blackish. Esophagus black, pyloric caeca black (sometimes appearing pale but with pigment on caeca and intestine) and at least the anterior part of the intestine black. Counts and measurements are given in Tables 1 and 2. Other features do not differ between the subspecies.

Material examined.—Holotype: LACM 35772-1, formerly UCR 328-3, an adult female, 209 mm, Costa Rica, 10 miles SW of Isla del Caño in 142 m, R/V TAURO sta. T-3, 15 July 1969.

PARATYPES: COSTA RICA: UCR 328-3 (4, 167–195) collected with the holotype. UCR 682-3 (1, 142) Costa Rica, Isla del Caño, Lat. 08°43′55″ N, Long. 83°57′52″W in 73–82 m, R/V SEARCHER sta. 480, 16 March 1975. PANAMA: UMML 32882 (1, 212) trawl "4°7°15°," no precise data,

but probably taken on same cruise as next collection, 11–13 Dec. 1969. GCRL 13965 (6, 169–217) and UP 807 (2, 169–189) Darien, between Pta. Ana Maria and Ensenada de Guayabo, M/V CANOPUS, 15 Dec. 1969. COLOMBIA: UMML 32229 (1, 232) Lat. 06°31.2′N, Long. 77°32.2′W in 205 m, R/V GILLISS sta. 15, 16 January 1972.

NON-PARATYPES: GCRL 13972 (1, 189, poorly preserved) Lat. 07°33′45″N, Long. 81°57′20″W, 4.5 mi. off Isla Coiba, Panama in 182–209 m, M/V CANOPUS, 6 June 1973.

Distribution.—*L. m. hubbsi* is known from northern Colombia to Costa Rica in 73 to 209 m. The shallowest station is near the head of a submarine canyon near Isla del Caño, Costa Rica. Water temperatures in this particular region probably are about 14°C at 75 m.

Etymology.—For Carl L. Hubbs, whose second scientific paper concerned a new cusk-eel from the eastern Pacific, in recognition of his many contributions to ichthyology and zoogeography.

Lepophidium microlepis inca new subspecies

Tables 1–2, Figure 1

Synonymy.—*Lepophidium microlepis*: Chirichigno F., 1968: 445–448, fig. 22 (first record for Peru; meristic and morphometric data for 2 specimens from Paita). Chirichigno F., 1974: 185 (in key to species of the genus *Lepophidium* from Peru; distribution in Peru).

Diagnosis.—Caudal vertebrae 59–62, total vertebrae 74–76, dorsal fin rays 135–141, anal-fin rays 116–121. Pyloric caeca 7–9. Vertical fins with conspicuous dark edge, this best developed in anal fin. Pectoral fins appearing clear but with light sprinkling of melanophores. Roof of mouth, upper pharyngeal region and gill bars blackish, the area sharply defined but the black on the roof of the mouth extending forward only about halfway along the inner edge of the palatine tooth patches. Esophagus black. Pyloric caeca and anterior part of intestines black. Counts and measurements are given in Tables 1 and 2. Other features do not differ between the subspecies.

Material examined.—HOLOTYPE: USNM 216345 a male, 193 mm standard length, Lat. 05°02′S, Long. 81°24′W in 195–316 m, ANTON BRUUN Cruise 16, sta. 627A, SOSC 289, 3 June 1966. PARATYPES: USNM 216346 (22, 132–191), UMML 32871 (5, 165–178), LACM 35562-1 (10, 161–182), CAS 33808 (10, 139–185) all collected with the holotype. IMARPE 1199 (1, 171) Paita, Peru, in 20–300 m, March 1965 and April 1966; 843 (2, 161–166) Lat. 04°48′S, Long. 81°17′W in 16 m, ANTON BRUUN Cruise 16, sta. 624b, 2 June 1966.

Distribution.—*L. m. inca* is known only from off northern Peru (Paira) in 16–320 m (see comments below under zoogeography).

Etymology.—For the tribe of the Incas.

DISCUSSION

Comparison of the Subspecies

Lepophidium microlepis hubbsi and *L. m. inca* share important pigmentary features lacked by *L. m. microlepis*. Although the esophagus is black in all three, only *hubbsi* and *inca* have the pyloric caeca and the small intestine black, the pigment being most intense in *inca*. Only one specimen of *hubbsi* has this area pale appearing but close examination shows many melanophores, a condition unlike that of *microlepis*. Similarly, *hubbsi* and *inca* have the gill bars, the upper pharyngeal region and the roof of the mouth brownish black (the pigment extending farther forward, to the vomerine teeth, in *hubbsi*), whereas this region is entirely pallid or only slightly dusky in *microlepis*. The pectoral fins are unpigmented in *microlepis*, lightly sprinkled with melanophores in *inca* and distinctly dusky in *hubbsi*. The dark border on the vertical fins is least developed in *microlepis*, usually present in juveniles but entirely absent from the dorsal fin in most adults, and inconspicuous in the anal fin in larger specimens. This border is better developed and persistent in both *hubbsi* and *inca* though it is most intense in *inca*.

All populations have 15 precaudal vertebrae, a few variants in each having 14. Numbers of caudal vertebrae and dorsal and anal rays are lowest in *microlepis*, highest in *inca* and intermediate in *hubbsi* (Table 2), although *hubbsi* more closely resembles *inca* in numbers of caudal vertebrae.

There is no subspecific variation in num-

Table 2. Meristic variation in subspecies of *Lepophidium microlepis*

	Dorsal Rays																								
	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141
microlepis	1	1	2	1	9	8	5	8	3	4	2*	1	–	–	–	–	–	–	–	–	–	–	–	–	–
hubbsi	–	–	–	–	–	–	–	–	–	–	–	1	1	1	2	6	2	2*	–	–	–	–	–	–	–
inca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	4	8	5	–	2*

	Anal Rays																								
	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121
microlepis	1	–	2	–	6	9	8	13	4	2	–	1*	–	–	–	–	–	–	–	–	–	–	–	–	–
hubbsi	–	–	–	–	–	–	–	–	–	–	–	2	3	5	3	2*	–	–	–	–	–	–	–	–	–
inca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	7	2	6	2	2*	1

	Vertebrae																										
	precaudal			caudal												total											
	14	15	16	51	52	53	54	55	56	57	58	59	60	61	62	66	67	68	69	70	71	72	73	74	75	76	77
microlepis	7	40*	–	1	10	17	16*	3	–	–	–	–	–	–	–	3	9	18	16*	1	–	–	–	–	–	–	–
hubbsi	5*	10	–	–	–	–	–	–	–	7	6	2*	–	–	–	–	–	–	–	–	1	8	6*	–	–	–	–
inca	2*	18	1	–	–	–	–	–	–	–	–	3	13	4*	1	–	–	–	–	–	–	–	–	3	14*	3	1

	Pyloric Caeca					Gill Rakers							Pectoral Rays†					
	5	6	7	8	9	9	10	11	12	13	14	15	21	22	23	24	25	26
microlepis	8	9*	2	1	–	–	3	7	6	3	2	1*	1	10	17*	10*	–	–
hubbsi	3*	4	6	1	–	2	1	2	3	1*	1	–	–	–	2	17	6*	3
inca	–	1	9	5*	1	2	8*	4	–	2	–	–	–	–	3	22*	4	–

* = lectotype (*microlepis*), holotype (*hubbsi*, *inca*)
† both fins counted

bers of gill rakers. *L. m. inca* averages higher in numbers of pyloric caeca but the distribution is skewed and the difference problematical. The higher average number of pectoral-fin rays in *inca* and *hubbsi* (both modally 24 versus 23 in *microlepis*) is more substantial but certainly of much less importance than the differences already discussed.

Meristic variation of *Lepophidium microlepis* as a whole equals or exceeds that of all other Pacific species of *Lepophidium* combined (Robins, 1962: Table 1) in dorsal rays, anal rays and caudal and total vertebrae even though three other species, *L. negropinna*, *L. pardale*, and *L. prorates*, are as wide ranging or nearly so. The variation in each subspecies of *microlepis* is, in contrast, quite comparable to that seen in the other species.

The morphometry of the various subspecies is presented in Table 1. Data for each subspecies are arranged according to increasing standard lengths. It can be seen by inspection that there is no noteworthy ontogenetic change within the size range studied. We purposely avoided measuring juveniles since it was not our intention (nor did we have sufficient material of all sizes) to study ontogenetic change.

Differences can be seen in eight characters. These differences are summarized in Figure 1. In three characters, pectoral-fin length, lateral-line length and bony interorbital width, *L. m. hubbsi,* though geographically intermediate, is extreme, in each instance having the larger measurement. *L. m. microlepis* and *L. m. inca* do not differ in these characters though larger samples may show that there is a significant difference between them in interorbital width. In the other five characters, *microlepis* has the highest and *inca* the lowest values. In predorsal distance, depth of body at the dorsal-fin origin and probably in post-orbital length of head, all three populations differ significantly. In head length, *inca* differs significantly from both *microlepis* and *hubbsi* which do not differ in this character. In depth of body at the anal fin, both *microlepis* and *inca,* though significantly different themselves, broadly overlap the intermediate *hubbsi.*

The characters discussed above do not show geographic variation in other species of *Lepophidium* studied to date.

Lepophidium m. microlepis, *L. m. hubbsi* and *L. m. inca* are very well differentiated subspecies differing in counts, body proportions and several pigmentary characters. In our opinion, the shared characters outweigh the differences when all species of *Lepophidium* are considered. Subspecific recognition seems to represent best our interpretations of the differences between these allopatric populations.

Within the eastern Pacific, *Lepophidium microlepis* shares most characters with *L. stigmatistium*, a species confined to the Gulf of California and the outer coast of Baja California. Although *L. stigmatistium* is sympatric with *L. m. microlepis*, the two are separate bathymetrically, *stigmatistium* occurring in shallower water. As noted below *L. stigmatistium* could be considered an earlier, fully differentiated stock of *L. microlepis* in the north. It is the only species of *Lepophidium* in the eastern Pacific that is so confined geographically.

Zoogeography

Lepophidium microlepis is one of three species of *Lepophidium* known to range from Baja California to Peru, the others being *L. pardale* (Gilbert) and *L. negropinna* Hildebrand and Barton. *Cherublemma emmelas* (Gilbert) is equally wide ranging and *Lepophidium prorates* (Jordan and Bollman) occurs from Baja California to Colombia. Yet, among them, only *L. microlepis* shows distinct latitudinal variation. The question is what isolating mechanisms are involved in separating the three populations of *L. microlepis*. Various authors (Clark Hubbs, 1952, 1953; Briggs, 1955; C. L. Hubbs, 1960; Rosenblatt, 1967; Dawson, 1975; and others) have discussed the distribution of shallow shelf and littoral fishes from this region. However, to our knowledge, no one

has considered geographic variation in deep shelf or upper slope species.

L. m. microlepis is restricted to the Gulf of California and the waters off the outer Baja California coast (see account under distribution of that subspecies, above). The shelf area off the mainland coast of Mexico virtually disappears between Puerto Vallarta (ca. 20°30′N) and the Gulf of Tehuantepec (ca. 16°00′N). Proper habitat for species that live on the deep shelf may be limiting in this region and this may account for the hiatus between the ranges of *microlepis* and *hubbsi*. Little is known of subsurface circulation of waters in this region. The prevailing surface current patterns in the eastern Pacific are important in determining the present distribution of the three subspecies of *L. microlepis* and the effects of these currents will be discussed later in this section. Important references on surface currents utilized in this discussion and not cited elsewhere in this paper are those by Bennett (1966), Blackburn (1962) and Wyrtki (1964, 1965).

Springer (1959) noted differences in the faunal composition in the tropical eastern Pacific and proposed a "Pacific Central American Faunal Gap" between "the middle of the coast of the Gulf of Tehuantepec, Mexico . . . and the Gulf of Fonseca, Nicaragua." If the current patterns of this region are considered, the predominant system influencing the area inhabited by *microlepis* (along the outer coast of Baja California) is the California Current which is destined to become the North Equatorial Current. The system influencing *hubbsi* (along the coast of Colombia and southern Central America) is the Equatorial Counter Current. These two opposing current systems may also be involved in the isolation of *microlepis* and *hubbsi* since larvae moving into geographically intermediate areas would be moved toward the open ocean with no chance to colonize favorable habitat. Sea surface temperature in the northern Colombia to Costa Rica region is significantly higher, and the surface salinity significantly lower, than off Baja California. Also, the annual variation of sea surface temperature in the northern region is greater than 6°C and less than 2°C in the south.

The distribution of the third and most southern species, *inca*, is poorly known. It apparently occupies a narrow zone in the Southern Hemisphere off the northern coast of Peru (from ca. 5°S to 10°S). This is entirely north of the area of separation of the Peruvian and Chilean components of the coastal circulation (Wooster, 1970). Most specimens of this subspecies were taken at depths in excess of 200 m indicative of an outer shelf–upper slope habitat. The shelf is much broader here than in areas immediately to the north and south. (Chirichigno F., 1968, gave the depth range as 20–320 m for IMARPE 1119 but this was a composite collection made in March 1965, and April 1966, and we assume that the three specimens of *inca* were from a haul in the deeper part of this range. IMARPE 843 is the shallowest (16 m) of a series of trawls hauled on that particular day. An error in handling material could have occurred but *inca* also might enter shallow water near drop-offs and where surface temperatures are low.) The surface current off Peru and Chile is the dominating Peru or Humboldt Current which leaves the coast at about 4°S to become the South Equatorial Current but there is some evidence that part of the flow goes into the Panama Bight, so mixing at the surface is conceivable. The subsurface flow is poorly known, especially in the Panama Bight. The coast of Colombia is influenced by the Equartorial Counter Current which reaches the coast at Colombia and swings northward paralleling the coast of Central America to southern Mexico. The Peru-Chile Undercurrent (Wooster and Gilmartin, 1961) is an important oceanographic feature off the section of South America inhabited by *inca*. This poleward flowing, nearly anoxic undercurrent may play an important role in isolating *inca*.

The most noteworthy difference between the regions north and south of the equa-

torial front at about 4°S (i.e., the hiatus between the territories of *inca* and *hubbsi*) is in surface conditions. Sea surface temperature in the north is high (greater than 25°C throughout the year) and salinity low (less than 33‰). To the south, in the Peru Current regime, sea surface temperatures are much lower (less than 20° except in January–March) and salinities higher (about 35‰). The two regions are separated at the surface by the strong equatorial front. Physiological differences in the larvae of *inca* and *hubbsi* could play a vital role in isolating these stocks. The region of hiatus between the ranges of the two subspecies is also one of narrow shelf although this is not so extreme as in the region between the ranges of *hubbsi* and *microlepis*.

The history of *Lepophidium microlepis* in the eastern Pacific is unknown. The genus is American and, despite identifications of fossil otoliths from elsewhere as those of *Lepophidium* and the recent, highly questionable attribution of a marketplace specimen of *L. cervinum* as being from the Tyrrhenian Sea (Nielsen and Bini, 1972), all evidence points to the genus originating in the Americas. The emergence of Central America in the Tertiary isolated stocks and no species of the genus is known to occur on both coasts of Central America. The Pacific species represent several lineages (Robins, 1962) and only *L. negropinna* has no close Atlantic cognate.

Lepophidium microlepis and *L. stigmatistium* (Gilbert) are closely related and either diverged after the emergence of the Central American barrier or represent separate invasions from what is now the Caribbean Sea.

One parsimonious explanation is that the ancestral stock was able twice to bridge unfavorable environments and currents to reach favorable habitats in the north, the first population differentiating fully as *L. stigmatistium* before *L. microlepis* arrived. The second invasion, according to our interpretation has only achieved subspecific differentiation. Similarly, *L. m. inca* represents a partially differentiated southern stock. According to this interpretation, *L. m. hubbsi* occupies the ancestral home of the species in the Pacific though it is not necessarily morphometrically the same as the ancestral stock or the least divergent.

The closest relatives of *microlepis* in the Atlantic represent undescribed species which will be treated subsequently by Robins.

Acknowledgments

This study stems from a program supported in the past by the National Science Foundation (NSF-GB28440), C. R. Robins, principal investigator. We are indebted to B. W. Walker (UCLA), R. J. Lavenberg and C. C. Swift (LACM), R. H. Rosenblatt, C. L. Hubbs and L. C. Hubbs (SIO), W. A. Bussing (UCR), and R. H. Goodyear (UP) for providing facilities, access to their collections, and other courtesies during our visits to their institutions, and for the loan of specimens. N. Chirichigno (IMARPE) loaned Peruvian material. L. W. Knapp (SOSC) provided a large Peruvian collection, C. E. Dawson (GCRL) loaned Panamanian material and Dr. L. Howell Rivero of Miami, Florida, kindly donated a Panamanian specimen. Drs. W. S. Wooster and G. L. Voss commented on oceanographic and zoogeographic aspects of this study. Most of our research was done at the senior author's home laboratory in Miami, Florida. This study is a contribution from the Rosenstiel School of Marine and Atmospheric Science, University of Miami.

It is a pleasure to dedicate this article and one of the new subspecies to Carl Hubbs, who has contributed so much to the ichthyology and zoogeography of the Pacific Coast of the Americas.

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DATE ACCEPTED: September 12, 1977.

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